Characterization of deposits of *Pomacea canaliculata* (Gastropoda: Ampullariidae) accumulated by snail kites: paleobiological implications

Características de los depósitos de *Pomacea canaliculata* (Gastropoda: Ampullariidae) acumulados por halcones caracoleros: implicaciones paleobiológicas

Claudio G. DE FRANCESCO*, Laura M. BIONDI** and Karina B. SÁNCHEZ**

ABSTRACT

We studied the main taphonomic attributes (breakage, orientation and size-frequency distribution) of modern shell piles of *Pomacea canaliculata* (Lamarck) accumulated by snail kites, in order to establish distinctive characteristics that allow the recognition of similar deposits in the fossil record. The study was conducted around three shallow lakes situated in southeastern Buenos Aires Province, Argentina: Los Padres (37° 56' S; 57° 44' W), Nahuel Rucá (37° 37' S; 57° 25' W) and Hinojales (37° 34' S; 57° 27' W). Shells were collected from three different types of piles: (1) on the surface in the littoral zone (2) underneath wire fences and (3) underneath trees. 63 % of predated shells had light damage on the outer lip, 17 % were intact. Dispersion of shells in each pile appeared to be related to the surface available to the snail kite for perching rather than to its relative height. Consumed shells varied from 23 to 66 mm indicating selection of sexually mature individuals by snail kites. In conclusion, the outer lip damage and size range of predated *P. canaliculata* shells are distinctive attributes that allow the recognition of similar deposits in the fossil record.

RESUMEN

Se estudiaron los principales atributos tafonómicos (fragmentación, orientación y distribución de tallas) de pilas actuales de *Pomacea canaliculata* (Lamarck) acumuladas por halcones caracoleros, para establecer características distintivas que permitan el reconocimiento de depósitos similares en el registro fósil. El estudio se llevó a cabo en tres lagos someros del sudeste de la provincia de Buenos Aires, Argentina: Los Padres (37° 56' S; 57° 44' W), Nahuel Rucá (37° 37' S; 57° 25' W) e Hinojales (37° 34' S; 57° 27' W). Las conchas fueron obtenidas de tres tipos diferentes de pilas: (1) sobre la superficie en la zona litoral (2) bajo alambrados y (3) bajo árboles. El 63 % de las conchas depredadas exhibió un leve daño en el labio externo, mientras que el 17 % permaneció intacto. La dispersión de las conchas en cada pila estuvo relacionada con la superficie disponible para el caracolero para movilizarse lateralmente más que con su altura rela-

* Centro de Geología de Costas y del Cuaternario, Universidad Nacional de Mar del Plata, CC 722, 7600, Mar del Plata, Argentina, CONICET. e-mail: cgdefra@mdp.edu.ar.
** Departamento de Biología, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Funes 3250, 7600, Mar del Plata, Argentina.

tiva. Las conchas consumidas variaron entre 23 y 66 mm indicando una selección por parte del caracolero de individuos sexualmente maduros. En conclusión, la fragmentación del labio externo y el rango de tallas de las conchas de *P. canaliculata* depredadas son atributos distintivos que permiten el reconocimiento de depósitos similares en el registro fósil.

INTRODUCTION

Pomacea canaliculata (Lamarck) is a freshwater snail native to South America, which is widely distributed throughout the Amazon Inferior Basin and the Plata Basin (CASTELLANOS AND FERNÁNDEZ, 1976). In recent years, *P. canaliculata* has received increased attention because it has become a serious pest in paddy rice in most Southeast Asian countries (HALWART, 1994; COWIE, 2002; WADA, ICHINOSE, YUSA AND SUGIURA, 2004), where the species was intentionally introduced in 1979 as a potential source of high protein food for local human consumption (DAMBORENEA AND DARRIGRAN, 2003). *Pomacea canaliculata* is recorded in Argentina since circa 11,000 ^{14}C years B. P. (PRIETO, BLASI, DE FRANCESCO AND FERNÁNDEZ, 2004) mainly in deposits from northeastern Buenos Aires Province (Salado and La Plata Basins). However, internal casts assigned to *Pomacea* have recently been recorded from early Eocene deposits (ca. 50 Ma) in central Argentina (MELCHOR, GENISE AND MIQUEL, 2002) which suggest an early origin for the genus in South America. Little is known about the paleoecological significance of holocene accumulations. A recent review of the paleontological literature available indicated that *P. canaliculata* displayed more restricted distribution and lower relative abundance in the past than in the present, probably due to a combination of megascale climatic and hydrographic changes (MARTÍN AND DE FRANCESCO, 2006).

A more rigorous testing of taphonomic and ecological traits through actualistic experiments or surveys is necessary to understand the ecological role of *P. canaliculata* in the past. Knowledge of the environmental or biological factors that may have restricted its distribution in the past may help to understand its modern spread. Predation by snail kites (*Rostrhamus sociabilis*, Vieillot 1817) is a possible biological factor that influences its distribution in native areas. The relation between shell form and predators has proven to be a very useful source of paleontological information that played an important role in our thinking about evolution (see VERMEIJ, 1987). Moreover, it is known that some predator species produce characteristic damage from which the predator can be recognised (CADÉE, 1994; 1995). In addition, shell repairs are indicative of unsuccessful predators (CADÉE, WALKER AND FLESSA, 1987; CADÉE, 1999a).

The snail kite is a highly specialized raptor that ranges from southern Florida and Mexico, throughout Central America, to Bolivia, Argentina and Uruguay (ANGEHR, 1999). It feeds almost exclusively on *Pomacea* although it will take other prey during droughts, including small aquatic snails, turtles and crabs (BEISSINGER, 1990). The snail kite displays a characteristic foraging behavior: it flies from 1 to 3 m above the water body in search of snails. Once a snail is detected, the kite descends to capture it, using its talons (BENNETTS, COLLOPY AND RODGERS, 1994). It then perches in order to extract the body from the shell with its hooked bill and discard the shells, which accumulate
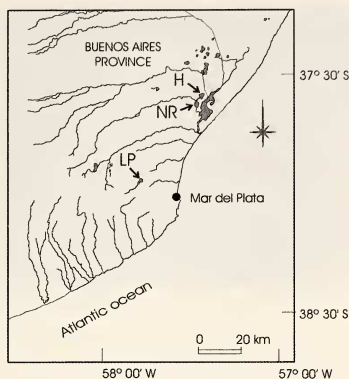
Figure 1. Location map: Hinojales lake (H), Nahuel Ruca lake (NR) and Los Padres lake (LP).
Figura 1. Mapa de ubicación: lago Hinojales (H), lago Nahuel Ruca (NR) y lago Los Padres (LP).

underneath, giving a record of the food eaten (HAVERSCHMIDT, 1970; COLLETT, 1977; BEISSINGER, 1983; SNYDER AND KALE II, 1983).

The limpkin (*Aramus guarauna*, Linnaeus 1766) has also been reported as a predator of *Pomacea* (COTTAM, 1936; COLLETT, 1977; REED AND JANZEN, 1999). Contrary to snail kites, the limpkin employs a wading foraging strategy, probing the bottom until its bill contacts a snail, which it then carries to a suitable elevated, flat spot on the marsh. Here, the bird hammers out the operculum with a sharp blow of the bill, and extracts the flesh. In doing so, the bill frequently makes a hole on the dorsal side of the shell, opposite the point of entry (COLLETT, 1977). These distinctive holes produced by limpkins on *Pomacea* shells may be easily recognized in the fossil record, giving direct evidence of the predatory activity of this bird in the past. Contrarily to limpkins, it has been pointed out from field observations that snail kites generally leave no marks at all (COLLETT, 1977; REED AND JANZEN, 1999). However, a detailed study on the characteristics of *Pomacea* piles produced by snail kites has not been carried out up to now.

In the present paper, we analysed the main taphonomic attributes (orientation, breakage, size-frequency distribution) of modern shell piles accumulated by snail kites in order to establish distinctive characteristics that would allow recognition in the fossil record. Moreover, recognition of *Pomacea* deposits would bring indirect evidence of the presence of this bird (or a bird with a similar foraging behavior) in the past, which has no fossil record in Argentina.

MATERIAL AND METHODS

Shell piles of *P. canaliculata* accumulated by snail kites were obtained during January-March 2003 around three shallow lakes of southeastern Buenos Aires Province, Argentina: Nahuel Rucá lake (37° 37' S; 57° 25' W), Hinojales lake (37° 34' S; 57° 24 'W) and Los Padres lake (37° 56' S; 57° 44' W) (Fig. 1). These shallow lakes comprise 245, 241 and 216 ha, respectively, and are characterized by an extensive littoral zone dominated by the aquatic macrophyte *Schoenoplectus californicus,* interspersed with relatively open water patches (GONZÁLEZ SAGRARIO, MIGLIO-

Figure 2. Outer lip damage produced by snail kites on *Pomacea canaliculata* shells. Photograph by Gabriela Hassan.
Figura 2. Fragmentación del labio externo producida por el halcón caracolero sobre las conchas de Pomacea canaliculata. *Fotografía por Gabriela Hassan.*

RANZA, AIZPÚN DE MORENO, MORENO AND ESCALANTE, 2002). Surrounding the lake are isolated native woods of *Celtis tala* (Nahuel Rucá and Hinojales lakes) and introduced forests of *Eucalyptus* sp. (Los Padres lake), which are used by snail kites as consumption sites. Annual average temperature in the area is 13.5 ºC, the minimum mean in July is 7 ºC and the high average for January is 19.2 ºC (GONZÁLEZ SAGRARIO ET AL., 2002). Annual average rainfall is 912-927 mm with most of the precipitation occurring from October to January (MIGLIORANZA, DE MORENO AND MORENO, 2004).

Shells were collected from 25 discrete piles created by snail kites (n= 300 shells) uniformly distributed among the three lakes, which were identified by direct observation of the foraging activity of birds. During the study, we did not observe the presence of limpkins in any of the three lakes or shell piles assigned to this species. Three types of piles were recognized: 1) shells accumulated on the surface in the littoral zone 2) shells accumulated underneath wire fences and 3) shells accumulated underneath trees. The taphonomic attributes analysed were: 1) fragmentation, 2) orientation and 3) size-frequency distribution. These attributes were selected because they are directly related to the foraging activity of snail kites, and

because they are easily recognized in modern and fossil shells.

The degree of fragmentation was scored on four relatively discrete breakage categories: 1) complete shells; 2) shells with broken aperture; 3) shells with broken body whorl and 4) shells wholly broken. The null hypothesis of a random distribution among the five categories of breakage was evaluated with a Chi-square test (ZAR, 1984).

The orientation of shells within each pile was assessed by two methods. The Distance to Nearest Neighbour (DNN, *sensu* CLARK AND EVANS, 1954) of total shells found in each pile was calculated as an estimate of dispersal. Differences in mean DNN values among the three types of piles were evaluated with a Kruskal-Wallis test (ZAR, 1984). A Tukey-type nonparametric multiple comparison test (ZAR, 1984) was used to determine significant differences between piles at p= 0.05. In addition, the proportion of shells oriented convex-up, convex-down, and oblique was calculated. The null hypothesis of a random distribution of proportions was evaluated with a Chi-square test (ZAR, 1984).

Size selection by the snail kite was evaluated by comparing the size ranges of predated shells in the three shallow lakes studied with previously published data on size of natural populations of *P*.
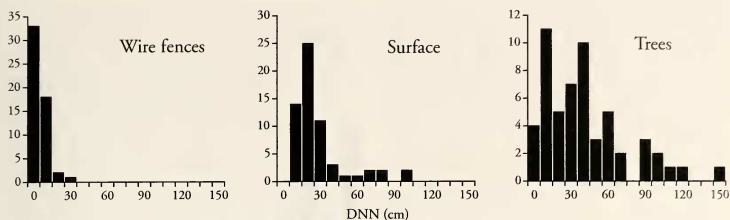
Figure 3. Distances to Nearest Neighbor (DNN) of shells accumulated underneath wire fences, on the surface of the littoral zone, and underneath tress.
Figura 3. Distancias al vecino más cercano (DNN) de las conchas acumuladas bajo alambrados, sobre la superficie de la zona litoral, y bajo árboles.

canaliculata from the area (MAPELLI, 2004). We measured total shell height to the nearest 0.1 mm with a digital caliper. In addition, the null hypothesis of no difference in the size-frequency distributions of predated shells among lakes was evaluated with a Kolmogorov-Smirnov test (ZAR, 1984).

RESULTS

The four categories of breakage were not randomly distributed in the shell piles (χ^2= 246.5; df= 3; p< 0.0001). The highest percentage (63 %) corresponded to shells with broken aperture, followed by 17 % that did not display any breakage at all. Nearly 14 % of shells displayed a broken body whorl and only 4 % of total shells were wholly broken. Apertural breakage consisted of light damage on the outer lip, in the area of continuous shell growth (Fig. 2), that was clearly recognizable as originated by kite predation after a careful scrutiny of shells.

DNNs varied significantly among piles (H= 70.5; df= 2; p< 0.0001). A gradual increase in DNNs from piles accumulated under fences to piles accumulated under trees was observed (Fig. 3). DNNs measured in piles accumulated under fences were significantly lower (1-2 cm) than those measured in all other piles (Tukey-type nonparametric test). Additionally, DNNs measured in piles accumulated on the littoral

surface (median= 17 cm) were significantly lower than those accumulated under trees (median= 37 cm). The proportion of shells convex-up, convex-down, and obliques showed no significant difference (χ^2= 1.51; df= 2; p= 0.47).

The size range of consumed shells varied from 23 to 66 mm, corresponding to sexually mature snails (ESTEBENET AND CAZZANIGA, 1992). Sizes were normally distributed in Nahuel Rucá lake and Los Padres lake (43.7 ± 8.1 mm and 45.6 ± 6.1 mm, respectively; dmax= 0.18; p> 0.10; Fig. 4) but were right-skewed in Hinojales (50.1 ± 8.9 mm; dmax= 0.57; p< 0.001; Fig. 4). Size-frequency distributions of natural populations of *P. canaliculata* in the area exhibited left-skewed curves with major peaks in 15-25 mm that gradually decreased towards sizes of 45-75 mm (MAPELLI, 2004). The comparison of size-frequency distributions between natural populations and predated deposits evidences selection on shell size by snail kites.

DISCUSSION

Our results indicate that modern shell piles accumulated by snail kites have distinctive taphonomic attributes that would potentially allow the recognition of similar deposits in the fossil record. Although not reported in previous works (HAVERSCHMIDT, 1970; COLLETT, 1977), most shells show frag-
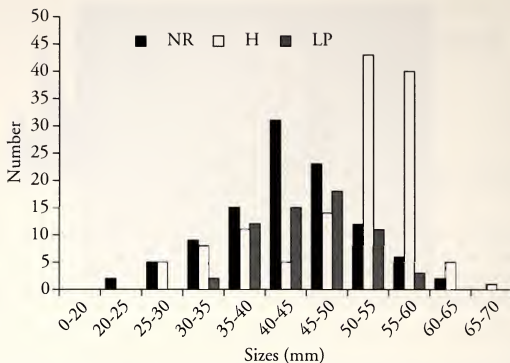
Figure 4. Size of predated *Pomacea canaliculata* shells in Nahuel Ruca lake (NR), Hinojales lake (H) and Los Padres lake (LP).
Figura 4. Tallas de conchas depredadas de Pomacea canaliculata *en los lagos Nahuel Ruca (NR), Hinojales (H) y Los Padres (LP).*

mentation along the shell margin, probably related to the action of the bird when pulling the soft parts out of the shell with the bill. It may be a consequence of the fact that the outer lip is a weak zone of continuous shell growth and, therefore, the calcium carbonate layer is thinner.

All piled shells exhibited a size selection towards adult snails. Several hypothesis have been proposed to explain this pattern. COLLETT (1977) interpreted it as a result of larger snails being easier for snail kites to see, or eventually, due to the fact that the kite's talons and bill are better suited for larger snails. This hypothesis is supported by the fact that *P. canaliculata* usually inhabits shallow, quiet and turbid sites close to the water surface (MARTÍN, ESTEBENET AND CAZZANIGA, 2001) where they are easily visible to snail kites from the air. Moreover, snails move periodically towards the water surface to breathe atmospheric air, increasing predation risk (COWIE, 2002). During spring and summer, females experience an additional predatory risk when crawling above the water level to lay eggs on emergent macrophytes (ALBRECHT, CARREÑO AND

CASTRO-VÁZQUEZ, 1996; ESTEBENET AND MARTÍN, 2002). On the other hand, BOURNE (1985) considered larger snails to be more profitable for snail kites than smaller ones. Despite the possible mechanisms involved, the size preyed by snail kites in unrelated environments suggests that these taphonomic attributes are characteristic of the species rather than ecological adaptation to particular conditions, which aids in the development of retrospective uniformitarian prediction.

The low percentage of shells with significant breakage found in piles may respond to taphonomic or biological causes. It may be possible that shells break when kites drop them from their perches after extraction, or by reworking once they are deposited on piles. Another possibility is failure in extraction by inexperienced recently fledged kites (SNYDER AND KALE II, 1983). In all cases, the resultant breakage of the shells might not be differentiated from deposition by natural processes. Even though different processes may explain significant breakage of shells, the low percentage in which breakage occurs makes it insignificant for paleobiological considerations.

The dispersion of shells in each pile appears to be related to the surface available to snail kites for perching rather than to its relative height. As wire fences limit the lateral mobility of the kite when perching, all shells discarded remain close to each other. On the other hand, the higher places for perching available along the littoral and in trees may explain the higher shell dispersal observed here. These results demonstrate that the separation between shells is not indicative of predated deposits (it may vary from 0 to 140 cm). We should expect to find past predated *Pomacea* shells as clumped concentrations in discrete stratigraphic levels or as isolated shells along a variable lateral extent. Moreover, the absence of a particular concavity orientation indicates that shells are randomly dropped after extraction and, therefore, this taphonomic attribute does not provide any evidence of past predated deposits.

CONCLUSION

The coincidence in both lip damage and shell size preyed by snail kites in unrelated environments suggests that these taphonomic attributes are characteristic of the species rather than ecological adaptations to particular conditions.

Therefore, it may be possible to infer the presence of snail kites in the past through the careful analysis of these taphonomic traits in fossil deposits. The results obtained here constitute an encouraging first step in making use of actualistic studies to infer past biological interactions in this particular predator-prey system. However, as shells deposited on land have a very low fossilisation potential (CADÉE, 1999b) the extent of retrospective uniformitarian prediction from the data obtained in the present work is somewhat limited and should be regarded with caution. Future work should be aimed at discriminating predated deposits from naturally accumulated assemblages in the fossil record.

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